EXPERIMENTS AND OBSERVATIONS

UPON THE

CIRCULATION IN THE SNAPPING TURTLE,

Chelonura Serpentina,

WITH

ESPECIAL REFERENCE TO THE PRESSURE OF THE BLOOD
IN THE ARTERIES AND VEINS.

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ON THE

CIRCULATION IN THE SNAPPING TURTLE.

Since the experiments of Hales in 1731, and the later and more accurate researches of Poiseuille, a number of observers have studied the blood-pressures in various vertebrate animals, among which may be mentioned the horse, dog, sheep, cat, rabbit, and bird. So far as I can discover, the only observations of this nature upon cold-blooded vertebrata were made by Volkmann, who experimented upon frogs and fresh-water fishes. No other similar examination of blood-pressures appears to have been made, and up to the present date no one has studied the subject in connection with reptiles of any kind.

The object of this memoir is to exhibit the results of a series of researches upon the blood-pressure in one of the most vigorous members of this class, the *Chelonura serpentina*, and thus to fill an important gap in our knowledge of hæmometry. The reptile in question is admirably suited for this purpose. It is strong, active, singularly tenacious of life, and may be procured easily of any weight up to twenty-five or thirty pounds. Inhabiting the waters of many of the streams and mill-dams in the Middle States, it may be readily had in excellent condition during the spring and summer, and for all purposes of physiological and toxicological research, may be made use of whenever it is desirable to replace the frog by an animal of greater bulk and superior tenacity of life.

The Snapping Turtles used in the following researches were brought from Havre de Grace on the Susquehanna river, and from the lower part of the State of Delaware, care being taken that only such were employed as had been captured by hand (dug out of the mud), rather than such as had been taken by the hook and line.

As I have alluded to the great strength and tenacious vitality of these creatures, it may be well to make some brief statement of a more distinct nature as to the extent to which they are endowed with these qualities.

A Snapper weighing twenty-seven and a half pounds was fastened by its tail to a ring,

and the blunt hook of a spring scale was caught in the upper jaw, the other end of the scale being also secured to the table. During this time the Turtle's head was held extended. When it was released the animal drew it briskly into the cover of the shell, thus pulling on the scale until the index-point marked fifty-seven pounds as the force of the pull made by the retracted neck. Nearly equal vigor was manifested by others of the same species, and all were so active that by extending the head and using their powerful tails they were able to right themselves with ease, when placed on their backs, a position in which the Green Turtle becomes altogether powerless.

The length of life in the separated head of the Snapper, and its power to bite long after being removed from the rest of the body, is very well known, but the astonishing resistance of the animal to one of our most active poisons is a still better test of its great and enduring vital power. So remarkable indeed was this, that I have studied it with some care, and described it at length in a separate paper. At present it will suffice to relate a single experiment illustrating the point in question.

Assuming M. Bernard's experiments* as a basis, if a Snapper weighing twenty-six pounds were a warm-blooded creature, it would be killed by the injection into its veins of about one-tenth of a grain of woorara. On several occasions I have injected into the jugular veins of Turtles weighing from twenty to twenty-seven pounds, thirty times this amount. The animal became motionless within five minutes, but soon began to recover, and at the close of twenty-four hours was, in several instances, as well as ever. As the heart's action is not primarily checked by this poison, which acts only on the motor nerves, it is gradually eliminated, and after some hours the power to move the respiratory muscles returning, the Turtle gradually recovers all its usual activity; the limit of endurance being the length of time during which the reptile can exist without renewing its supply of oxygen. I have occasionally seen Turtles weighing two or three pounds, so poisoned with woorara as to remain motionless and without the least reflex movement during three days, after which life and action gradually but completely returned.

It will thus be seen that for strength and tenacity of life, the Snapper is well suited to exhibit a type of reptilian blood-pressures.

The following points were made the subjects of study:

1st. The arterial pressure.

2d. The force of the heart's contraction.

3d. The effect of inspiration and expiration on the arterial pressure.

4th. The influence of muscular motion on the arterial blood-pressure.

5th. The blood-pressure in the central and distal ends of divided veins.

6th. The effect of muscular exertion on the venous pressures.

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* Sur les substances toxiques, etc. Paris, 1857, p. 335.

The instrument used in the following experiments was the hæmometer of Magendie, as modified by M. Bernard.* The blood was kept fluid by filling the caoutchouc tube of the instrument with a saturated solution of carbonate of soda, which was found to displace two millimetres of mercury in the registering tube. Accordingly a reduction to this extent from the record of blood-pressure has been made in each instance. Any further description of an instrument so well known to physiologists would be altogether unnecessary.

EXPERIMENT.—Turtle weighing twenty-two pounds, from Delaware. Temperature of air 73° F. Present, Messrs. Keene, Stone, and Cantrell. The Turtle having been properly secured so as not to impede the circulation or respiration, a tube was placed in the left femoral artery and connected with the caoutchouc tube† of the hæmometer, when the following record was obtained after a few minutes' repose:

TIME.	PRESSURE.		REMARKS.
	Minimum.	Maximum.	
4.41 P. M.	30 M.M.	40 M.M.	Pulse 28 to the minute.
4.42	35	45	Respiratory act.
4.44	33	43	
4.46	33	45	Slight respiration.
4.47	30	38	
4.49	36	43	Respiratory act.
4.50½	32	40	
4.52½	27	37	After respiration.
4.53	33	42	Cleaned tube, no clot in it.
4.56	29	38	
4.57	28	37	When violent movements took place, during which the pulse became too irregular for notation. The extremes reached, were
	23	49	
4.57½	26	35	No clot in tube.
4.58	27	37	
	28	37	
	25	33	
	30	40	A full respiratory act.
5.6	28	37	After respiratory act.
	30	42	
5.12 to }	27	37	
5.15 }	29	37	Pulse 28. During respiration and violent motion, the limits were
	29	43	
During several minutes,	29	36	Steady pulse.

June 18th, 1861. Present, Messrs. Keene, Stone, and Cantrell.

EXPERIMENT No. 2.—Temperature 71° F. Snapping Turtle. Weight twenty-two

* Leçons sur les Propriétés Physiologiques et les Altérations Pathologiques des Liquides de l'Organism, par M. Cl. Bernard.—T. I, p. 167. Paris, 1859.

† This tube was so thick as to withstand perfectly the dilating force thus brought against it.

pounds.   The left carotid artery was isolated without loss of blood, a tube secured in the opening, and the following record obtained:

TIME.	PRESSURE.		REMARKS.
	Minimum.	Maximum.	
6.3½	37 M.M.	47 M.M.	
6.6	35	44	
6.6½	35	44	
6.10	35	44	
6.11	36	47	Respiratory act.
6.18	32	38	
6.18½	30	37	
6.26	33	41	Tube cleaned. Minute loose clot in artery.
6.29	36	46	
6.29½	41	53	Respiratory act.
6.32½	36	46	
	49	59	After violent movement and repeated respiration.
	32	43	Steady and regular.

The above observations are given in full, as an example of the mode of conducting the experiments.   In every case, the extreme pressures were noted; but no complete record was kept of the influence of every respiratory act or muscular movement.   Very little trouble was given by the clotting of the blood in the vessel or tubes, and even when clots did form, they were so loose in texture as scarcely to interfere with the registration of pressure.

In the experiments of Poiseuille, Volkmann, and Vierordt, the mean between the extremes of the rise and fall was given as the standard of arterial blood-pressure, and the instrument used was some form of Poiseuille's hæmadynamometer.   M. Bernard has since shown that the hæmometer of Magendie, which he terms the cardiometer, is a better instrument for exhibiting the changes of circulation with rapidity and exactness, and that, moreover, its registration gives higher numbers for the pressures than the older instrument.   Having made use of the same apparatus in my own researches, I have preferred to follow M. Bernard's method of notation, which may be easily explained in a few sentences.

This distinguished observer states that when the cardiometer is connected with the artery of an animal the mercury rises to a varying height, which he calls the arterial pressure, believing it to be due, in part at least, to the elasticity and vital contractility of the arterial walls.   Each pulse of the heart elevates the column of mercury to a certain point above this, whence again it falls during the diastole of the ventricles.   The excess of mercury thus lifted he takes to represent the power of the heart's systole.   Both of the numbers thus obtained may vary with the individual and with the respiratory and other movements of the body.   M. Bernard holds the view that the arterial tension is not due alone to the injecting power of the heart, and that certain agents, which alter the heart-force, do not diminish the arterial tension, whilst other substances which plainl-

lessen the arterial tension, do not alter the power of the central propelling organ. Most physiologists are of opinion that the intersystolic pressure is indirectly, but alone due to the action of the heart, the arteries only restoring to the blood, so to speak, the excess of power employed in their distension, during the contraction of the cardiac pump. Thus, if in the case of a warm-blooded mammal, the mercury of the manometer should rise to 100 m.m., and at each heart-pulse leap to 120 m.m., falling during the diastole again to 100 m.m., M. Bernard would describe the arterial pressure as represented by the weight of a column of mercury of a 100 m.m., and would estimate the heart-force at 20 m.m., M. Poiseuille, on the other hand, would give the average, or 110 m.m., as representing the circulatory pressure.

Further research is needed before this question can be settled, and as the difference is merely one of mode of statement, I have preferred to follow M. Bernard's method of notation, without feeling pledged to the correctness of the views upon which its practice is founded.

The following results were obtained from observation of the pressure of the blood in the carotid arteries of eight Snapping Turtles, every possible precaution being taken to prevent loss of blood or injury to nerves and veins while insulating the artery. The numbers here given are those which were noted when the Turtle was in repose and not breathing. As the respiratory acts occurred at intervals of from one to three minutes, observations were easily obtained during these periods of repose.

No. 1. Snapping Turtle. Weight 23 lbs. Temp. of air 71° F. Pulse 25. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
35 M.M.	45 M.M.	10 M.M.
35	44	9
35	44	9
32	38	6
30	37	7
32	43	11
Mean, 33.2	41.8	8.6

No. 2. Snapping Turtle. Weight 20 lbs. Temp. 72° F. Pulse 29. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
39 M.M.	48 M.M.	9 M.M.
41	53	12
41	53	12
38	47	9
39	47	8
39	50	11
33	47	14
37	44	7
Mean, 38.4	48.6	10 2

No. 3. Snapping Turtle. Weight 26½ lbs. Temp. of air 76° F. Pulse 31. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
29 M.M.	42 M.M.	13 M.M.
29	43	14
29	38	9
28	38	10
26	37	11
22	33	11
20	30	10
24	34	10
23	32	9
29	39	10
24	34	10
Mean, 25.7	36.3	10.6

No. 4. Snapping Turtle. Weight 24½ lbs. Temp. of air 72° F. Pulse 27. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.		DIFFERENCE.
33 M.M.	49 M.M.		16 M.M.
34	51		17
33	49		16
31	46		15
30	47		17
33	51		18
31	46		15
34	47		13
33	45		12
34	47	Pulse 32.	13
33	43		10
Mean, 32.6	47.3		14.7

No. 5. Snapping Turtle. Weight 21 lbs. Temp. of air 77° F. Pulse 40. A tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
34 M.M.	47 M.M.	13 M.M.
33	50	17
42	58	16
36	49	13
37	49	12
41	53	12
42	51	9
37	51	14
Mean, 37.7	51	13.3

No. 6. Snapping Turtle. Weight 20 lbs. Temp. 79° F. Pulse 36. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
40 M.M.	56 M.M.	16 M.M.
37	50	13
37	50	13
37	52	15
37	52	15
Mean, 37.6	52	14.4

No. 7. Snapping Turtle. Weight 19½ lbs. Temp. of air 74° F. Pulse 30. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
30 M.M.	39 M.M.	9 M.M.
36	47	11
29	40	11
31	41	10
31	41	10
32	43	11
Mean, 31.5	41.8	10.3

No. 8. Snapping Turtle. Weight 19½ lbs. Temp. of air 74° F. Pulse 30. The tube was placed in the left carotid:

MINIMUM.	MAXIMUM.	DIFFERENCE.
39 M.M.	45 M.M.	6 M.M.
39	44	5
35	45	10
30	41	11
30	39	9
35	44	9
31	40	9
Mean, 34.1	42.5	8.4

Upon comparing the above records, it will be seen that the mean of the minimum pressures is 33.8; that of the maximum 45.1; and that of the difference 11.3. The first number, therefore, represents the average height of a column of mercury sustained by the arteries during the diastole of the heart, the average effect of the systole being to lift the column 11.3 m.m. higher. The statements in regard to the blood-pressures in mammals vary so much that it is not easy to find a standard of comparison with those of chelonians; but, assuming M. Bernard's observations to be correct, we find that the minimum of pressure in the arteries is nearly the same in mammals of all sizes, being about

110 m.m. in the horse.
103 m.m. in the dog.
95 m.m. in the rabbit.

The rise caused by the heart-beat bears, however, a greater relation to the size of the animal, and is noted in the above animals as 65, 12, and 5 respectively. The minimum pressure in the artery of the Snapping Turtle is, therefore, about one-third that in the

artery of a mammal, or as 33.3 to 110, 103 or 95, according to the animal chosen for comparison.

The force of the heart-act in the Turtle elevates the column, on an average, 11 m.m., which is about the pressure observed in a dog of middle size when tranquil, and when the respirations do not prevent accurate observation of the influence of single pulsations, as is commonly the case.

Upon reviewing these results, it is hardly possible to escape the conviction that the capillary circulation must for some reason be more easily carried on in the Turtle, or else that in this animal the arteries are more relaxed than in the dog for example, and less contractile than in mammals of like weight. In cold-blooded vertebrates, such as the frog and fresh-water fish, M. Volkmann[*] found the arterial pressures to vary between 18 m.m. and 84 m.m.

The impulse conveyed to the column of blood during the systole of the heart in the Turtle is somewhat different from that of the mammal. In place of a sudden and abrupt motion, as seen in these latter animals, the mercury moves so slowly that the time of its rise during a systole may be estimated at one second, the period of fall being one second and one-fifth. The rise of the mercury was usually steady and regular; its fall was broken and irregular, so that after falling two-thirds of the distance rapidly, an equal time was occupied in effecting the remaining third of the total descent. The number of heart-pulsations varied in the eight animals examined from 25 to 40. In the individual cases its number was scarcely altered during the whole observation.

The same regularity did not prevail in the circulating current, and, apart from the influence of respiration and muscular motion, it may be seen that the pressure varied from time to time, owing to causes which I was unable to understand.

EFFECT OF INSPIRATION, EXPIRATION, AND MUSCULAR MOTION ON THE ARTERIAL PRESSURES.

Before considering these points it will be proper to make a brief statement as to the mechanism of the respiration in the Snapper. All of the leading authorities on the physiology of chelonian reptiles describe their respiration as effected by an act of deglutition similar to that which occurs in the batrachia.[†] However this may be in some chelonians, I have arrived at the conclusion that in the Snapper the respiratory movements are entirely effected by abdominal or thoracic organs, and that their type is that of the mammal rather than that of batrachians. If, for example, the Turtle's mouth remains open it breathes as usual, which would be impossible were its respiration effected by an action of swallowing the air or of forcing it into the lung, according to the usual statement.

* Volkmann. Die Hämodynamick.
† Milne Edwards. Leçons sur le Physiologie, etc., Paris, 1858. Tome II., 2d partie, p. 387.

To settle the question more completely I cut the trachea of a Snapper across, and still found that the breathing went on at the ordinary rate. Next, a bent glass tube, two millimetres in width, was adapted to the upper end of the divided trachea and allowed to dip into water. The water rose and fell in the tube about one millimetre only at each respiratory motion, and even this was clearly due to the synchronous reflex movements in the laryngeal muscles, which open and shut the glottis during the act of breathing,—a circumstance which is also observed to take place in higher vertebrates, as Dr. Dalton has well shown.

Lastly, the bent tube was adapted to the lower end of the divided trachea and again dipped in water. At each inspiration the fluid was largely drawn up into the lung and rejected again during the subsequent expiration. It is, therefore, impossible to concede that this type of respiration is any other than that which is seen in mammals, and we must admit at once that the whole respiratory movement is effected in the Snapper as in them by the agency of thoracic and abdominal groups of muscles.

I have, elsewhere, shown more fully the mode in which they effect this end and the part played by the various muscles thus employed.

Respiration occurs in the Snapper about once in a minute in some cases, and often less, as once in two or two and a half minutes in others, while this animal undoubtedly has the power to exist a long time without breathing, when the process would involve inconvenience.

The respiratory process consists first of a full expiration, which is followed at once by a long and very large inspiration, and that again by a short and incomplete expiration, which still leaves the lungs more or less full until the time for the next respiratory movement arrives, when again a long expiratory act begins it.

During the interval between two respiratory acts, a slight pulsatile motion is visible in the space between the two limbs and the carapax and plastron. This movement appeared to be respiratory in its character, and to test the correctness of this view I resorted to the following plan.

Experiment.—A large tube was placed in the lower end of the divided trachea, and a smaller glass tube* fitted to it and bent at an angle of 45 degrees. The open end was allowed to rest in water. In the intervals between the full respirations above described, the water rose and fell in the tube about 3 to 4 m.m., and this movement corresponded with the motion observed on the flanks of the animal. It was, however, so small in amount, the tube being only 2 m.m. in width, that it could scarcely be said to effect any change of moment in the mass of air in the lungs, and at the utmost could only be efficient in shifting slightly the air in contact with the various parts of the breathing

* 2 millimetres wide.

surfaces. A very simple experiment finally decided the nature of the motion above described.

EXPERIMENT.—A tube having been placed in the right carotid artery was connected with the hæmometer. A second tube, fitted to the cut trachea, was so bent as to be allowed to dip just below the surface of a vase of water. On bringing the arterial and tracheal tubes near together, the rise and fall of the fluids in both was found to be exactly synchronous. The pulsatile motion perceived in the flanks and transmitted through the lungs, as shown above, seems, therefore, to be due to the propagated impulses from the neighboring vessels, and, perhaps, in part also from the pulmonary arteries.

During the interval between two respirations the column in the hæmometer tube rose and fell with singular steadiness at times. The long expiration which begins the series of respiratory motions, had no marked effect on the column sustained. The long inspiration which followed caused a small rise in the mercury, and the short incomplete expiration which terminated the series of movements raised it still higher.

The following experiment will serve to exemplify the amount and character of this influence.

Snapper. Weight 19½ lbs. Temp. 70° F. Pulse 33. Tube in the left carotid:

TIME.	MINIMUM.	MAXIMUM.	DIFFERENCE.	RESPIRATORY STATE.
4.10 P. M.	34 M.M.	45 M.M.	11 M.M.	
4.12	34	44	10	Expiration.
	36	46	10	Inspiration.
	40	51	11	Short expiration.
4.14½	33	40	7	Expiration.
	33	41	8	Inspiration.
	39	49	10	Short expiration.

In mammals it is easy to see why active expiration should cause an increased pressure in the arteries, since the thorax is contracted and the belly drawn in so as to exert considerable compression upon the large arteries, and thus to cause an instant rise in the manometric column of mercury attached to an artery. In the Turtle the first respiratory act is a slow one, and the amount of force employed in effecting it but small; whence no marked influence is visible in the arteries. The long inspiration which follows usually increases a little the arterial pressure, although sometimes, where the action of breathing is not energetic, no such effect can be seen. The cause of the slightly increased pressure alluded to above I have been unable to fathom. The short expiration which completes the respiratory series at once raises the arterial pressure. This is, probably, due to the fact that at this time the lung distended with air is favorably situated to exert direct pressure on neighboring vessels, and also to the fact that this final expiratory motion is vigorous and abrupt.

The effect of muscular movement upon the pressure of the blood in the arteries was well marked and interesting. During violent movement the force of the heart remained unaltered, but the whole column of mercury rose, a result which attained to a maximum when the movements were coincident with the long inspiration and the short expiration which terminate each single series of respiratory movements. On such occasions the mercury sometimes rose as high as 70 m.m. and the action of the heart was irregular and unequal in force. Immediately after the movements were over, the mercurial column fell to a much lower point than usual, and then gradually ascended to the normal standard, as illustrated by the following record.

EXPERIMENT.—Snapper. Weight 24½ lbs. Temp. of air 78° F. Tube in left carotid. Not all the respiratory acts were here noted:

TIME.	MINIMUM.	MAXIMUM.	
4.45	33 M.M.	49 M.M.	
4.47	34	51	
4.48	33	49	
	20	50	During violent struggles the heart acting irregularly.
4.55	31	46	Pulse 27.
5.06	33	51	Free movement.
5.11	31	46	
5.13	15	70	Prolonged movements and active respirations, during which this rise took place.
	31	46	
5.21	34	47	Movement.
5.27	27	33	
5.28	31	40	Movement very violent.
5.29	10	18	
5.34	32	44	
5.34½	33	45	Pulse 28.

VENOUS BLOOD-PRESSURES.

The arrangement of the veins of the neck in the Snapper favor peculiarly an examination of the blood-pressures, since they are so large and numerous that an interruption of the current in one of them does not at all interfere with the general flow of blood towards the heart.

Both carotids are accompanied by one large internal jugular vein, and sometimes by two. The external jugular is also very large, and the œsophagus is surrounded by a plexus of anastomosing veins of large dimensions. At the back of the neck there are also one or two dorsal veins of considerable size.

EXPERIMENT.—Turtle. Weight 20 lbs. The tube was placed in the distal end of the internal jugular vein, when the mercury rose to 6 m.m. and was seen to pulsate feebly, the column rising about ⅓ m.m. at each heart-pulse. Violent motion raised the column to 11

m.m. in one case and to 14 m.m. in another.   Pulse 29.   The carotid artery at this time exhibited a pressure of from 41 to 53 m.m.

EXPERIMENT.—Turtle.   Weight 20 lbs.   The tube having been placed in the distal end of the vessel, the column rose to 5 m.m.   Slight pulsation of ⅓ to ½ m.m.   During muscular action it rose to 28 m.m.   Pulse 36.   The tube was next placed in the cardiac end of the cut vein, when it rose to 3 m.m. and pulsated about 1½ m.m.   Similar results were obtained upon further experiment.   When the tube was placed in the distal end of a large vein, the average height of column of mercury supported was 6.7 m.m.   In the cardiac end of the same veins the average was 3 m.m.   In all cases muscular motion elevated the column from 11 to 30 m.m.

It will be seen above that a pulsation of feeble character took place even when the distal end of the vein was examined.   This singular phenomenon appears to be a normal occurrence in the larger veins of the neck.   In those of the limbs it was scarcely perceptible, but in the neck it was always visible, and was well marked in the great veins, and best of all in the external jugular.   At first I supposed it to be due to the pulsation of neighboring arteries, or to the transmission through anastomotic channels of the pulse which is noticed when the lower or cardiac end of a vein is the subject of study.   The first of these possibilities is negatived by the fact that the pulsation was still seen where the vein chosen was remote from any large artery, which is the case with the external jugular vein.   The second is disposed of by making use of the dorsal vein or external jugular far up in the neck, and where it is thus remote from large communicating branches.

The pulsation referred to is, in all probability, due to the propagation of the heart-force through the capillary system into the veins.   The venous pulse which was observed in the cardiac end of the veins of the neck, was not visible in the veins of the limbs.   It was due, no doubt, to the pulsatile action of the walls of the vena cava, so well described by Alison.

Muscular movements, as in other animals, increased the venous pressure considerably. The influence of the respiratory acts on the venous circulation was imperfectly studied, owing to a failure of proper material, and is, therefore, reserved for future study.